SILURIAN CRINOIDS FROM
THE PENTLAND HILLS, SCOTLAND

by JAMES C. BROWER

ABSTRACT. The crinoid fauna of the Pentland Hills consists of six species, of which five are new: *Macrostylocrinus silurocirrifer, Ptychocrinus longibrachialis, Dimerocrinites pentlandicus, Herpetocrinus parvispinifer*, and *Dendrocrinus extensidiscus. Pisocrinus campana* Miller is also known from the Silurian (upper Llandovery to Ludlow) of the North American Mid-continent. Pentland Hills crinoids are generally rare and show low taxonomic diversity compared to many crinoid faunas of similar age, suggesting a marginal habitat for crinoids. The most likely unfavourable conditions are quiet water, high suspended sediment content, rapid sedimentation, and perhaps influxes of brackish water. Study of the phylogeny of *Dimerocrinites pentlandicus* shows that the zygodiplobathrid base can be derived from the eudiplobathrid type by reducing the growth rates of the basals. *Macrostylocrinus silurocirrifer, Ptychocrinus longibrachialis*, and *Dendrocrinus extensidiscus* belong to archaic lineages which began in the Ordovician. Elsewhere, their relatives became extinct before the upper Llandovery.

THE marine Silurian of the Pentland Hills, near Edinburgh, consists of three inliers, of which the North Esk Inlier is the largest and most important. Since 1861 about thirty identifiable crinoids have been collected from the North Esk Inlier by various workers. Most of these specimens belong to the John Henderson and David Hardie Collections in the Royal Scottish Museum (RSM). Despite the rarity of crinoids, several investigators have recorded specimens and these are tabulated below with the writer's annotations, except that duplicate citations and vague determinations such as 'crinoid stems', etc., are omitted:

Periechocrinus. Salter (*in* appendix to Howell and Geikie 1861, p. 134). Unidentifiable stem.

Periechocrinus, from the 'Starfish Bed', in the Hardie Collection (Peach and Horne 1899, p. 593). This collection has been examined; neither *Periechocrinus* nor anything labelled such has been found. Probably the specimen is referable to one of the camerate crinoids described later in this paper.

Periechocrinus sp. from Zone C of Henderson and Brown along River North Esk (Peach and Horne 1899, p. 596). Specimen apparently lost.

Periechocrinus moniliformis from the Lyne Water (Peach and Horne 1899, p. 602). Institute of Geological Sciences, Edinburgh (GSE 12792). Unidentifiable arm fragment.

Pisocrinus cf. *campana* from the *Plectodonta* Mudstones along the River North Esk (Lamont 1952, p. 29). RSM 1970.42.2–4. Assigned to *P. campana* Miller.

Myelodactylus? fragments from the Deerhope Burn Flagstones (Lamont 1954, p. 272). RSM 1970.42.1. Unidentifiable arm fragment.

Cyathocrinites sp. from Wetherlaw Linn (Wilson and Smith 1962, p. 138). GSE 12790. A paratype of *Macrostylocrinus silurocirrifer* sp. nov.

The total Silurian crinoid fauna of the Pentland Hills consists of six identifiable species. In addition there are one or two indeterminable inadunate crinoids.

For a general account of the geology and stratigraphy of the North Esk Inlier in the Pentland Hills, the reader should consult Mykura and Smith (1962) and Mykura (1960, the localities containing the crinoids are shown on the geological map on

p. 166). More detailed discussions are available in Lamont (1947, 1952). The age of the marine Silurian within the Pentland Hills has been controversial and various workers have proposed ages ranging from Ludlow (Howell and Geikie 1861, pp. 4–6) to upper Llandovery. Present practice assigns the crinoid bearing beds within the North Esk Inlier to the *crenulata* Zone of the latest Llandovery (Cocks *et al.* 1971, p. 118, fig. 6).

PALAEOECOLOGY

Lamont (1952) discussed the palaeoecology of the entire Silurian sequence of the Pentland Hills. The sediments are chiefly clastic; grits, a few quartzose sandstones and conglomerates, numerous wacke-sandstones, siltstones, mudstones, and shales. The predominant colours are brown, green, red, and purplish-grey. The over-all impression of the Silurian in the North Esk Inlier consists of a basin-filling sequence. The Llandovery rocks represent a complex series of predominantly marine habitats which formed at variable depths near a shifting shoreline. Brackish water and perhaps non-marine conditions developed, especially in the later phases of deposition. The Wenlock sediments are mostly red and green clastics which contain fish, plants, and *Spirorbis*. This sequence is interpreted as non-marine or perhaps brackish water.

Burial conditions. The internal skeleton of crinoids is mesodermal and occupies the bulk of that layer. The various plates are held together by muscles, ligaments and, in some cases, interlocking articular surfaces. After death the muscles and ligaments decompose and the plates begin to disarticulate (see Brower 1973, pp. 269–271 for more details). The attack of scavengers also tends to break up and fragment dead and possibly dying crinoids. Living crinoids are known to be scavenged by brittle-stars and various crustaceans. Once the crinoid skeleton falls apart, wave and current action tend to separate the various plates, depending on sizes and shapes. Thus the preservation type allows a rate of burial gradient to be determined for a single habitat. Completely preserved specimens represent the most rapid burial whereas fully disarticulated ones indicate slow burial in which decomposition was complete before entombment. The terms rapid and slow are purely relative, and under high agitation conditions rapid burial would be faster than under lesser agitation. The Pentland Hills crinoid localities fall into three types which are listed from least to most rapid burial:

1. Isolated columnals only. Calyx and arm plates are conspicuously lacking. The columnals are usually well sorted and mainly found on bedding planes. These are believed to have been transported.

2. Debris consisting of loose calyx plates, columnals, arm plates, small arm fragments, and short stem segments. These may be on bedding planes or within sedimentation units. This occurrence represents individuals which had partially decomposed and broken up, although burial took place prior to complete decomposition and hydraulic separation by waves and/or currents.

3. More or less complete crowns. The arms are mostly or completely preserved. Long stem segments may be found attached to the dorsal cup or the stem segments are closely associated with the crowns. Several calyces without stems or arms are

known, although these are rare. Isolated plates of any type are uncommon. Examples seen by the writer are found both within sedimentation units and on bedding planes. Burial was undoubtedly prior to significant decomposition.

Living conditions. The presence of crinoids denotes near normal salinity. All known living crinoid faunas are found in normal marine waters although minor influxes of brackish waters may sometimes occur. Contrary to popular belief, there is some experimental evidence which indicates certain Recent species are able to tolerate appreciable intervals of slightly brackish or hypersaline water. Clark (1917, p. 188) subjected several individuals of *Tropiometra carinata* (Lamarck) to salinities of about $27\%_{00}$ (slightly brackish) and roughly $41\%_{00}$ (slightly hypersaline) for 12 hours; the crinoids survived and thrived when returned to normal marine water. Similar non-quantitative results were obtained by Clark (1915) on other species. On the Blake cruises of 1877–1879, Captain Sigsbee and A. Agassiz placed some living animals in a tank of iced fresh water and the specimens endured for several hours (Carpenter 1884, pp. 332–333). In view of the palaeogeography of the Pentland Hills, normal marine conditions are postulated, but influxes of brackish water are quite possible.

The Pentland crinoid habitats were clearly subtidal, as living crinoids cannot survive periods of dessication. The main morphological aspects of the Pentland crinoids are small size and fragile crown habit, which suggests quiet water conditions when compared to many other Palaeozoic crinoid localities. This is also consistent with the predominantly fine-grained texture of the sediment in which the crinoids mostly occur, i.e. mudstones and siltstones, although a few specimens are known from fine sandstones.

Several features suggest that the Pentland habitats were marginal for crinoids. First is the general rarity of crinoids, in conjunction with their low taxonomic diversity (six species). This is considered low diversity relative to other occurrences of about the same age, for example: Girardeau Limestone (upper Ordovician, Illinois and Missouri) eighteen species; Brownsport Formation (Ludlow, Decaturville, Tennessee area) over forty species; Rochester shale (Wenlock, Lockport, New York) about thirty-five species. Second is the high abundance of 'evolutionary relics'. Three of the crinoids, *Macrostylocrinus silurocirrifer*, *Ptychocrinus longibrachialis*, and *Dendrocrinus extensidiscus*, belong to lineages which began during the Ordovician. Elsewhere, these lines of evolution seem to have died out prior to the upper Llandovery. Lastly, the Pentland specimens of *Pisocrinus campana* are probably dwarfed compared with normal individuals from North America. Thus the small size and fragile nature of the crinoids implies quiet water conditions, which in conjunction with the sediment, the particles suspended in the water, and the rapid sedimentation postulated by Lamont (1952), may have been the main unfavourable factors. Most Recent crinoids living in shallow waters prefer moderate to strong agitation which ensures a continual fresh supply of dissolved oxygen and planktonic food, while at the same time preventing deposition of sediment (Fell 1966).

Most of the crinoids occur in the Gutterford Burn 'Starfish Beds' in close association with starfish. The starfish diversity exceeds that of crinoids by seven species to four. As usual in clastic 'starfish beds' with crinoids, the starfish individuals greatly

outnumber the crinoids, by more than ten to one in this case. *Dictyocaris* fragments (kindly identified by Dr. C. D. Waterston) are moderately abundant. Other groups less commonly associated with the crinoids are graptoloid and dendroid graptolites, echinoids, various brachiopods including *Lingula* and *Glassia compressa*, a few trilobites, and worm trails. It might be thought that some of the starfish were preying on the crinoids. However, this seems unlikely because living crinoids are conspicuously avoided by most predators such as fish, starfish, and echinoids. The occurrence of moderately abundant *Dictyocaris* is also noteworthy. The material is fragmented and may have been transported to the burial site. Alternatively, the organisms may have been living with the crinoids. The probability of transportation is difficult to evaluate for such fragile specimens. Størmer (1935) believed *Dictyocaris* lived under brackish and/or freshwater conditions, and *Dictyocaris* occurs in nonmarine rocks of the Old Red Sandstone. If the Pentland *Dictyocaris* were living with the crinoids, normal marine conditions are clearly implied by the crinoids.

The crinoids from the *Plectodonta* Mudstones along the River North Esk and other localities occur with a different fauna. *Dictyocaris* and starfish have not been observed, and the fauna is dominated by marine brachiopods, trilobites, lamellibranchs, gastropods, and cephalopods.

TERMINOLOGY

Generally, the terminology follows that of Moore (1952, text-fig. 18-2; 1962). The proximal plate of the camerate *CD* (posterior) interray is designated primanal, following Jaekel (1918, p. 28). Brachials rigidly incorporated into the dorsal cup are termed fixed-brachials. The ray orientation system is that of Carpenter (1884, text-fig. 2). The *A* and *C* rays of Carpenter correspond, respectively, to the anterior and right-posterior rays of most authors. The interray areas are designated by the flanking rays; for example, the posterior interray which lies between the *C* and *D* rays is the *CD* interray. The other interrays are not differentiated, but referred to as lateral interrays; the interrays included in this category are *AB*, *BC*, *AE*, and *DE*.

The camerate crinoids described here have two to four free arms in each ray. Two-armed species show two half-rays; the area between these and the equivalent position in four-armed crinoids is termed an interhalf-ray, the calyx plates of which are intersecundibrachs. In four-armed taxa, two half-rays are present, each consisting of two free arms called quarter-rays. The space between two quarter-rays is designated the interquarter-ray and its plates are intertertibrachs. All plates located between the rays are interbrachials. These include interray plates occurring between the radials, primibrachs, secundibrachs, etc. The camerate plate sequence directly overlying the primanal is the anal series, the elements of which are anal-series plates. From proximal to distal, the anal series plates are designated secundanals, tertanals, quartanals, etc. The anal series is generally separated from the *C* and *D* rays by *CD* interray interbrachials.

SYSTEMATIC PALAEONTOLOGY

Subclass CAMERATA Wachsmuth and Springer, 1885
Order MONOBATHRIDA Moore and Laudon, 1943
Suborder GLYPTOCRININA Moore, 1952
Superfamily PATELLIOCRINICAE Ubaghs, 1953
Family PATELLIOCRINIDAE Angelin, 1878
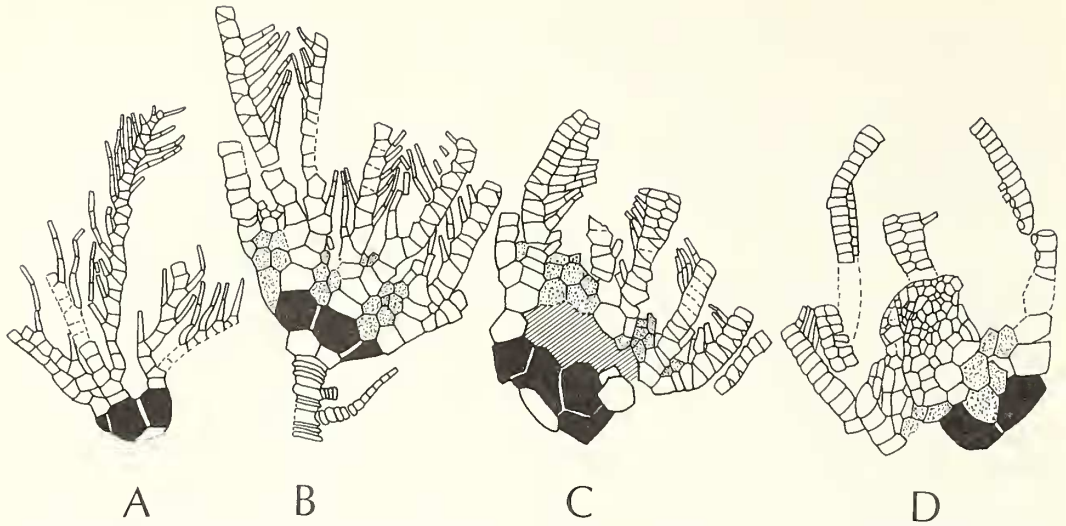MACROSTYLOCRINUS Hall, 1852

Type species. M. ornatus Hall, 1852.

Macrostylocrinus silurocirrifer sp. nov.

Plate 73, figs. 1, 2, 4; Plate 75, figs. 4, 5; text-fig. 1

1962   *Cyathocrinites?* sp. Wilson and Smith, p. 138.

Holotype. Royal Scottish Museum (RSM) 1885.26.78b, a well-preserved crown.

Paratypes. Crowns: RSM 1897.32.292, Institute of Geological Sciences, Edinburgh GSE 12791. Internal mould of partial calyx, GSE 12790. Stem segments: RSM 1897.32.293, 294, 295, 296, and 300; 1885.26.78c, d.

Type localities. Gutterford Burn Flagstones, 'Starfish Bed', Gutterford Burn. Deerhope Burn Flagstones, River North Esk, at bend 935 yd N. 30° W. of North Esk Cottage. Probably Henshaw Siltstone, Wetherlaw Linn, left bank, 340 yd upstream from River North Esk.

Diagnosis. A species of *Macrostylocrinus* characterized by numerous small nodes on calyx plates, nodes range from round to elongate; brachials covered with granules, round nodes, elongate nodes or sinnous ridges in adult. Two biserial arms per ray of mature biserial brachials in adult. Column bears long slender cirri.

Description of adult. Calyx cone shaped with straight walls and narrow base, height/width roughly 0·6. Ornament of median-ray ridges and numerous small nodes, nodes range from round to elongate, nodes on the median-ray ridges tend to be elongated parallel to the ridges, ornament on brachials of fine granules, round nodes, elongate nodes or fine sinuous ridges, tegmen plates covered with small nodes. Cirri ornamented with nodes or elongate striae. Basal circlet high, visible from side of calyx. Radials largest plates in calyx. Primibrachs two, smaller than radials; primibrach *1* hexagonal; primibrach *2* axillary, with five or seven sides. Three or four secundibrachs fixed into calyx by interbrachials. Interbrachials large, regular, one plate in first range, followed by several ranges of two or three plates. Intersecundibrachs few, comprised of several ranges which consist of one or two plates each. Tegmen plates moderately large, irregularly arranged. Anal opening and posterior interray not observed. Arms two per ray, erect, pinnulate. Proximal brachials uniserial, becoming more wedge-shaped distally. Next are several brachials of immature biserial type, proximal and distal margins curved. Distal brachials are of the mature biserial type; proximal and distal margins straight, differentiated from inner margins. Proximal pinnule located on secundibrach *2*, all higher brachials with pinnules. Pinnules long, slender, composed of long angular pinnulars. Column round with crenulate sutures, axial canal not seen. Nodals bearing long slender cirri, roughly twice as high as internodals, with nodose margins. Internodals with central sharp ridges, thin, lacking cirri. Cirri round, long, slender, flexible, consisting of up to forty cirrals. Distal part of stem unknown.

Ontogeny. The three crowns which range from about 1·8 mm to 12·5 mm in calyx height illustrate some aspects of development (Pl. 73, figs. 1, 2, 4; Pl. 75, fig. 5; text-fig. 1). The growth patterns closely parallel those of *M. pristinus* Brower (1973, p. 371). Free brachials were incorporated into the calyx by means of interbrachials throughout ontogeny. The primibrachs comprise the highest fixed-brachials in the lateral interrays of the smallest animal. By the time a calyx height of 12·5 mm was attained, secundibrach *3* was fixed into the calyx and at least four ranges of interbrachials occurred. As in most similar camerates, the formation of intersecundibrachs followed a similar path. In the smallest crinoid the two secundibrachs *1* of the same ray are not joined. Following this, the proximal margins of these two plates grew into lateral contact after which intersecundibrachs began to appear. The oldest crinoid had the lower part of secundibrach *4* fixed into the calyx in this way. The origin of the fixing interbrachials and intersecundibrachs remains uncertain; they are believed to represent interambulacral plates of the tegmen. During plate accretion the diameter of previously formed nodes was augmented while new nodes developed along the outer margins of the plates.

All free brachials of the smallest crinoid are uniserial, wedge-shaped, relatively high, and angular with prominent pinnule facets. The largest crinoid exhibits three types of brachials. The proximal plates are uniserial; these are succeeded by several immature biserial plates (proximal and distal margins are curved) which are followed by numerous mature biserial brachials (proximal and distal margins are straight). Basically, the proximal parts of the arms of the largest crown retained the same configurations seen in the youngest specimen. Conversely, the distal brachials developed from the uniserial to the biserial type. The

TEXT-FIG. 1. *Macrostylocrinus silurocirrifer* sp. nov. A, lateral view of immature crinoid, paratype GSE 12791, note small number of fixed-brachials and uniserial arms, × 5·5. B, lateral view of more mature specimen with more extensive fixed-brachials and arms consisting of predominantly immature biserial brachials, holotype, × 3. C, D, lateral views of crushed crown of adult with biserial arms, paratype RSM 1897.32.292, × 2, lateral interray (counterpart) and tegmen (part) views, respectively. Symbols: radials black, interbrachials stippled, damaged parts of specimen are obliquely ruled.

mature brachials are wider relative to their height and the pinnule facets are smaller compared to the total size of the brachials than in the youngest specimen. Consequently the adult brachials present a much smoother outline.

Column growth can only be examined by comparing stem segments of different diameters. Inasmuch as the columnal widths were augmented during ontogeny, wider stem segments are considered older than narrower ones. Examination of the proximal part of the stem (diameter 1·5 mm) in the holotype reveals the following formula for nodals (N) and internodals (IN = internodals which are numbered as follows, 1IN = priminternodal, 2IN = secundinternodal, 3IN = tertinternodal, etc.): 2IN–2IN–1IN–2IN–N–2IN–1IN–2IN–N–2IN–3IN–1IN–3IN–2IN–3IN–N. This suggests that the nodals, priminternodals, and probably the secundinternodals formed directly under the calyx whereas the tertinternodals originated below the calyx by intercalation between previously formed columnals. This seems reasonable because all columnal orders that were initiated below the calyx should appear in the first cycle of plates. The oldest column segment, diameter 2·0 mm, shows the following: N–5IN–4IN–3IN–4IN–2IN–4IN–3IN–4IN–1IN–4IN–3IN–4IN–2IN–4IN–3IN–4IN–5IN–N. Thus the nodals and four orders of internodals were fully developed and a fifth order of internodals was beginning to appear. Almost 80% of the columnals grew by intercalation between older plates whereas only about 20% formed immediately below the calyx.

A proximal cirrus on the holotype has only eight cirrals. Those of the largest column segment are much

PLATE 73

BROWER, Scottish Silurian crinoids

longer being composed of up to forty plates. Thus new plates formed throughout ontogeny which augmented the cirrus length. Cirral lengths remained nearly constant in all specimens and length growth of individual cirrals was not important in formation of longer cirri. Presumably, the new cirrals were added at the distal tips like new brachials and pinnulars in the arms.

Comparison. M. silurocirrifer is most similar to *M. cirrifer* Ramsbottom (1961, p. 20) from the Ashgill of Girvan. The two species resemble each other in having two biserial arms in each ray, similar calyx ornament consisting of median-ray ridges and numerous small nodes, and a stem with cirri. The two forms can only be distinguished by the nature of the cirri. Those of the Pentland crinoid are long and slender. The ratio of cirrus length/column diameter ranges from about 17 to 23 when complete cirri are seen. The Girvan species bears heavier cirri which are shorter relative to column diameter; cirrus length/column diameter equals a maximum of 10. Judging from the observed orientations of cirri, those of *M. silurocirrifer* were more flexible than those of *M. cirrifer*. The Pentland species is easily separated from all *Macrostylocrinus* except *M. cirrifer* by the calyx ornament. Stems with cirri are only seen in *M. cirrifer* and *M. silurocirrifer*.

Phylogeny. Morphological comparison and stratigraphic position indicate that *M. silurocirrifer* was probably a lineal descendant of *M. cirrifer*, after which this lineage became extinct. All other Llandovery and Wenlock macrostylocrinids were probably derived from *M. pristinus* Brower of the upper Ordovician of North America. The only other British form is *M. anglicus* Jaekel (1918, p. 36), from the Wenlock at Dudley, which probably evolved from a North American crinoid of Llandovery age such as *M. laevis* Springer (1926*b*, p. 26). Certainly the Wenlock species was not descended from *M. silurocirrifer*. The separation between the *M. cirrifer*-*M. silurocirrifer* lineage and that of the other macrostylocrinids may be related to substrate type in which the former lineage adapted to living on sand, silt, and clay substrata while the latter was restricted to limestones and shaly limestones.

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Order DIPLOBATHRIDA Moore and Laudon, 1943
Suborder EUDIPLOBATHRINA Ubaghs, 1953
Superfamily DIMEROCRINITICAE Ubaghs, 1953
Family DIMEROCRINITIDAE Bassler, 1938
PTYCHOCRINUS Wachsmuth and Springer, 1885

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Type species. Gaurocrinus splendens Miller, 1883.

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Ptychocrinus longibrachialis sp. nov.

Plate 74, fig. 3; text-fig. 2

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Holotype. University of Edinburgh, Grant Institute of Geology 134, 135 (part and counterpart).

Type locality. Unnamed argillaceous sequence above Gutterford Burn Flagstones; Gutterford Burn, mudstone layer just above top plantation.

Diagnosis. A species of *Ptychocrinus* with two long and slender arms in each ray. Free brachials much higher than wide. Pinnules small and slender.

Description. Calyx incompletely known, conical with straight walls and narrow base, height/width ratio about 0·7. Ornament of ill-defined median-ray ridges, plate sutures depressed.
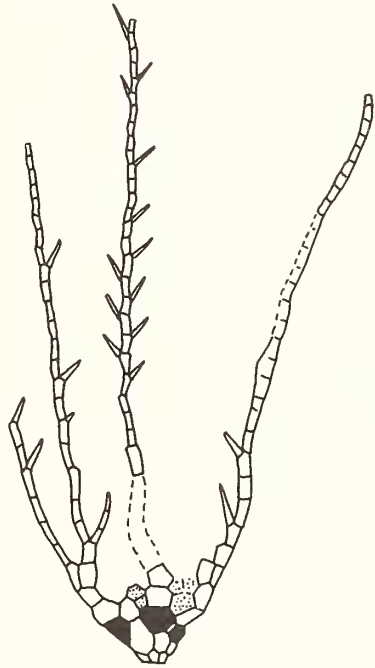   Infrabasals small, pentagonal, roughly equidimensional, visible from side of calyx. Posterior interray

basal large, septagonal, higher than wide, distally truncated for reception of primanal. Other basals smaller, hexagonal, higher than wide. Radials with seven sides, wider than high. Primibrachs two, equidimensional; primibrach *1* hexagonal; primibrach *2* axillary, septagonal or pentagonal. Distal fixed-brachial is probably secundibrach *1*. Interbrachials large, regular, one hexagonal plate located at level of primibrach *1*, second range consists of two plates at level of primaxil, higher ranges not preserved. Intersecundibrachs not present. Posterior interray not completely known; primanal separates posterior radials, primanal slightly higher than wide, with seven sides. Arms two per ray, long, slender, composed of uniserial free brachials. Free brachials much higher than wide, height/width ranges from 2·0 to 3·0. Proximal pinnule occurs on interray side of secundibrach *2*. Pinnules small, slender; number of pinnulars in each pinnule uncertain, probably two or three; pinnulars long, slender, with round backs. Only proximal part of stem preserved, column flattened but originally was probably round, cirri lacking. Nodals and priminternodals with nodose margins, secundinternodals with central sharp ridges.

Comparison. Aside from the Pentland crinoid, three species of *Ptychocrinus* are known, all of which occur in upper Ordovician rocks of the North American Mid-continent. The Pentland animal is most similar to *P. fimbriatus* (Shumard) (1855, p. 194; Brower 1973, p. 446). Both forms bear two arms in each ray and show the same type of ornament consisting of well-developed median-ray ridges with otherwise smooth or granulose plate surfaces. In juvenile and mature individuals of *P. fimbriatus*, the widths of the free brachials equal or exceed the heights thereof, except for a few of the proximal and distal plates. All free brachials of the Pentland crinoid have slender outlines with heights greatly exceeding the widths.

P. parvus (Hall) (1867, p. 304; see Wachsmuth and Springer 1897, p. 199) has a similar calyx to *P. fimbriatus* in both ornament and plate shapes. This American crinoid typically exhibits four unbranched arms per ray although a few half-rays failed to bifurcate during ontogeny. Secundibrach *2* or rarely secundibrach *3* forms the axillary. Only two arms per ray are found in *P. longibrachialis* sp. nov. The calyx ornament of *P. splendens* (Miller) (1883, p. 230; Wachsmuth and Springer 1897, p. 198; Brower 1973, p. 448) is comprised of strong stellate ridges in contrast to the median-ray ridges and smooth plates of the Pentland crinoid. Both forms possess two arms in each ray. Those of *P. longibrachialis* are unbranched, whereas those of *P. splendens* branch twice, proximally on secundibrachs 12–16 and on the distal tertibrachs in mature individuals.

TEXT-FIG. 2. *Ptychocrinus longibrachialis* sp. nov., *C* ray view of holotype, note long slender arms consisting of elongate brachials and comparatively small cup, ×3·7. Symbols: radials black, interbrachials stippled.

Phylogeny. Comparative morphology and stratigraphic position indicate that the Pentland form was a lineal descendant of the upper Ordovician *P. fimbriatus*. The ontogeny of the ancestor is well known (Brower 1973, p. 448). *P. longibrachialis* evolved from the ancestral form by means of growth divergences of the brachials. In *P. longibrachialis* the free brachials are about twice as wide as high but *P. fimbriatus* exhibits roughly equidimensional plates. Thus

the brachials of the Pentland crinoid were probably derived from those of *P. fimbriatus* by increasing the growth rates of height and decelerating the growth vectors of width as soon as the brachials formed at the arm tips, after which this growth pattern continued. The shape differences of the brachials caused a correlated change in arm length. Equivalent-sized crinoids of the two species have about thirty to forty secundibrachs in each arm. Consequently the arms of the Pentland crinoid ranged longer than those of an ancestor of the same size. The main adaptative significance of this change was most likely related to food gathering and respiration. The number of feeding tube feet was roughly similar in the two forms because most primitive lower Palaeozoic camerates have four to five sets of covering plates on each brachial and pinnular. However, the longer arms of *P. longibrachialis* must have allowed the animal to drain a larger area of water than an equivalent-sized *P. fimbriatus*. Also the surface area of the arms was greater in the Pentland animal, which would have aided respiration in a quiet-water habitat which was poorly oxygenated. Long slender arms of this type are fairly common in lower Palaeozoic crinoids found in such environments.

DIMEROCRINITES Phillips, 1839

Type species. D. decadactylus Phillips, 1839.

Dimerocrinites pentlandicus sp. nov.

Plate 74, fig. 5; text-fig. 3*a*

Holotype. RSM 1885.26.78h, an external mould of a cup showing parts of two rays and two interrays.

Type locality. Gutterford Burn Flagstones, 'Starfish Bed', Gutterford Burn.

Diagnosis. A questionable dimerocrinitid with slender, conical cup. Median-ray ridges poorly defined, plates of cup finely granulose. Base of cup is of zygodiplobathrid type in which the radials rest directly on the infrabasals, basals are small rectangular plates located in interradial position between the radials and infrabasals. Primibrachs with eight or nine sides. Interbrachials numerous with four ranges of plates below the proximal secundibrachs, proximal two ranges consist of one plate each, higher ranges composed of two or more plates. Arms unknown but calyx structure indicates that four fixed-arms were present, secundibrach 2 axillary.

Description. Cup cone-shaped with straight walls and narrow base, height/width 1·4. Median-ray ridges present but are poorly defined, plates covered with numerous fine granules, column facet has prominent rim. Infrabasals large, high, consisting of six-sided plates, height/width 1·2. Radials large, resting on distal margins of truncated basals, eight-sided, height/width 1·4. Basals small, located in interradial (zygodiplobathrid) position, inserted between the radials and basals, basals with four sides, height/width 1·5. Primibrachs two, roughly equal to the radials in size, height/width ranges from 1·2 to 1·5; primibrach *1* octagonal; primibrach *2* eight- or nine-sided, axillary. Two secundibrachs present with the second axillary; secundibrach *1* larger than secundibrach *2*, height/width 1·4; secundibrach *2* approximately equidimensional. Roughly three tertibrachs fixed into the calyx, uniserial, slightly wedge-shaped, wider than high to equidimensional. Proximal interbrachials mostly large, regular; one pentagonal plate in each of the first two ranges, second range terminates at level of primibrach *1*; third and fourth ranges occur between primaxils, two plates present in third range, fourth range made up of two or three large plates, two small supplementary plates observed in one interray. Higher ranges of interbrachials less regular than proximal ones, four or five ranges present, each of which bears three or four plates, higher interbrachials terminate at level of tertibrachs. Intersecundibrachs present, three ranges known, one plate in each range. Arms and tegmen not

seen. Proximal part of column preserved; columnals round, height/width about 0·14, columnal margins are nodose.

Remarks. *D. pentlandicus* is unique in two respects. First is the structure of the cup base. The basals are small relative to the infrabasals. Consequently, the basals comprise small rectangular elements inserted between the infrabasal and radial circlets. The radials rest directly on the truncated infrabasals and the basals are not in lateral contact (text-fig. 3*a*, *g*). Most other dimerocrinitids possess a eudiplobathrid base in which the basals are large in conjunction with relatively small infrabasals. Therefore, the basals are in lateral contact and the radial circlet rests on the basals (text-fig. 3*f*). The cup base of *D. pentlandicus* is like that of zygodiplobathrids, such as *Cleiocrinus* and *Spyridiocrinus* (text-fig. 3*d*) except that the proximal interbrachials do not separate the radials in the lateral interrays. The second difference is the shape of the primibrachs and the associated interbrachials. The primibrachs have eight or nine sides in contrast to the four to seven sides of typical dimerocrinitids. Consequently, there are more ranges of interbrachials in *D. pentlandicus* than in typical dimerocrinitids. The Pentland crinoid has four ranges of interbrachials below the proximal secundibrachs whereas normal dimerocrinitids have only one, two, or three ranges in the equivalent position.

The Pentland species is different enough from normal dimerocrinitids for a new genus to be proposed for *D. pentlandicus*. This is not done here because the species is only known from one side of a single calyx which lacks the arms and most of the stem. If a new genus were proposed it could not be fully defined based on the present material.

Origin of zygodiplobathrids. Before discussing the affinities of the Pentland crinoid, the ancestry of zygodiplobathrids must be reviewed. Breimer (1960, pp. 256–257, text-fig. 5) documented variation in the Devonian rhodocrinitid, *Rhipidocrinus crenatus* (Goldfuss). All crinoids studied have the radials separated by the proximal interbrachials. The specimens range from those with all radials resting on truncated infrabasals and small quadrangular basals inserted between the proximal parts of the radials (zygodiplobathrid type, text-fig. 3*d*) to typical rhodocrinitid types (text-fig. 3*c*) where the basals are large, in lateral contact, and support the radials and interbrachials. Transitional crinoids are also known. Note that small basals (relative to size of the infrabasals and radials) are associated with the zygodiplobathrid condition and large basals with the normal rhodocrinitid or eudiplobathrid base. Ubaghs (1950, p. 120) notes that two of the radials of *Paulocrinus biturbinatus* Springer (1926*b*, p. 21, pl. 4, figs. 5, 5*a–c*) lie on truncated infrabasals whereas the other three rays have the normal rhodocrinitid condition. As in *Rhipidocrinus crenatus*, the relatively large infrabasals and small basals are associated with the zygodiplobathrid type base. These examples clearly support Ubaghs (1950) and Breimer (1960) in their contention that zygodiplobathrids and normal dicyclic camerates are both variants of the same basic organization. It also implies that one was probably ancestral to the other. These variations within rhodocrinitids are believed to indicate genetic instability with respect to this character, at least in certain species. On the other hand, the proximal structure of the cup seems to be stabilized in zygodiplobathrid taxa. Although these crinoids are rare and do not seem to have been successful, moderately large
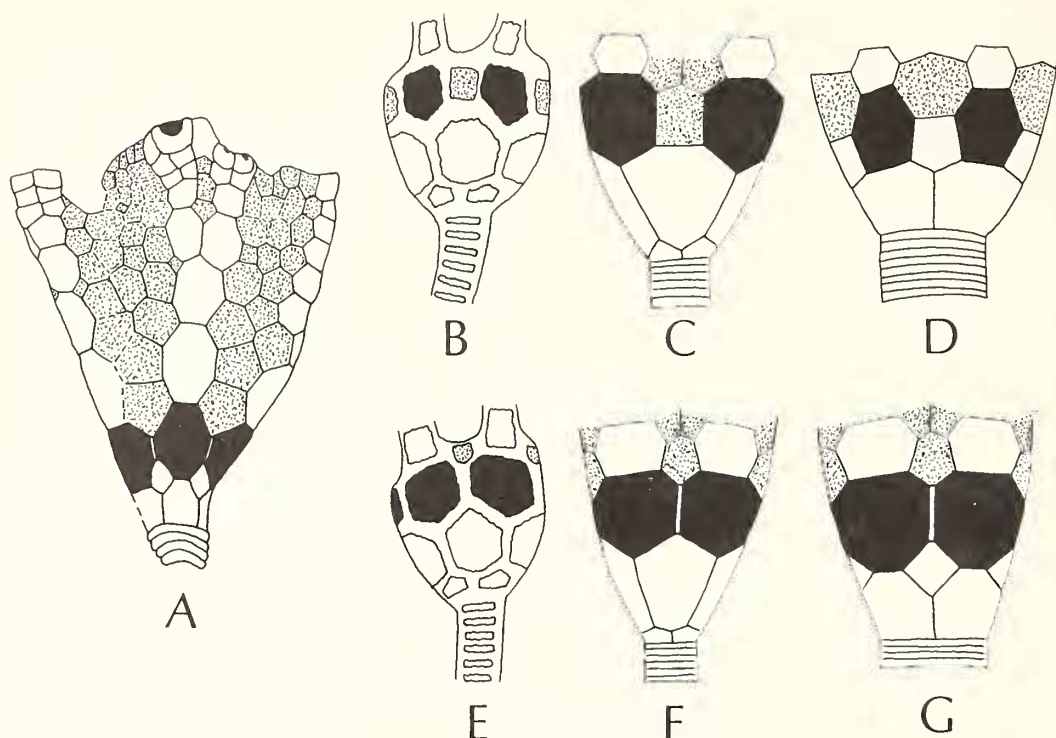
TEXT-FIG. 3. Origin of *Dimerocrinites pentlandicus* sp. nov. A, lateral view of holotype; note shape of primi-
brachs, structure of interbrachials, and zygodiplobathrid base, ×3·4. B–D, sketches showing probable
ontogeny of rhodocrinitids with eudiplobathrid base and zygodiplobathrids. B, 'larva' of dicyclic camerate
crinoid with interbrachials separating the radials; note that the plates are still separated by tissues; during
later ontogeny, these join to form a rigid mosaic of plates; reconstructed by analogy with living crinoids,
based on the growth sequence of plates and statistical data of Brower (1973, pp. 292–328); height of larval
calyx is about 0·5 mm. C, D, bases of mature crinoids simulated by growth of the 'larva'. C, eudiplobathrid
base of rhodocrinitid, growth rates of height and width of the plates relative to total size of the calyx:
infrabasals 0·14, basals 0·43, radials 0·43. D, zygodiplobathrid base, relative growth rates of height and width
of the plates: infrabasals 0·62, basals 0·13, radials 0·25. E–G, sketches showing postulated ontogeny of
zygodiplobathrid base seen in *D. pentlandicus* sp. nov. and normal dimerocrinitids. E, 'larva' of dicyclic
camerate crinoid in which the proximal interbrachials are at the level of the primibrachs, reconstructed as
before. F, G, bases of mature dimerocrinitids simulated by growth of the 'larva'. F, eudiplobathrid base of
normal dimerocrinitid, relative growth rates for plates: infrabasals 0·14, basals 0·43, radials 0·43.
G, zygodiplobathrid base of *D. pentlandicus* sp. nov., relative growth rates for plates: infrabasals 0·62,
basals 0·13, radials 0·25. All relative growth rates of plates are approximate averages for both height and
width. Symbols: radials black, interbrachials stippled.

samples are available in *Cleiocrinus laevis* Springer (1911, p. 44). Examination of five to ten calyx bases discloses no variation.

The oldest zygodiplobathrid is the bizarre *Cleiocrinus* from middle Ordovician rocks of North America (Springer 1905; Ubaghs 1950, pp. 116–120; 1953, p. 691). In *Cleiocrinus*, the combined radial-basal circlet overlaps and hangs down over the infrabasals. Except for the *CD* interray, there are no interbrachials and the adjacent ray plates join one another above the radials and basals. The calyx is large because of the numerous fixed-brachials and all calyx plates are pierced by complex sutural pores which are interpreted as respiratory devices connected to body coeloms. The free arms are composed of uniserial pinnulate brachials. The evolutionary history of *Cleiocrinus* is unknown because there are no known connecting links between the genus and any known Ordovician archaeocrinids or rhodocrinitids. Nevertheless, *Cleiocrinus* is believed to have been derived from an archaeocrinid or rhodocrinitid stock.

The Devonian zygodiplobathrid *Spyridiocrinus* is less obscure (see detailed discussion in Ubaghs 1950). Aside from the large basal concavity and a reduced number of interbrachials, intersecundibrachs, etc., the over-all crown habit of *Spyridiocrinus* is 'typical rhodocrinitid'. Comparison of *Cleiocrinus* and *Spyridiocrinus* shows only one similarity—the zygodiplobathrid base. Consequently the two crinoids are not considered closely related. Obviously, the bizarre *Cleiocrinus* was not ancestral to *Spyridiocrinus*. The large time gap between the two taxa is certainly consistent with this belief. The total morphological similarities between *Spyridiocrinus* and Silurian–Devonian Rhodocrinitidae seem much greater than those between *Spyridiocrinus* and *Cleiocrinus*. The most similar rhodocrinitid genera are: *Anthemocrinus* Wachsmuth and Springer (1881, p. 208 (382)), Wenlock. *Paulocrinus* Springer (1926b, p. 22), middle or upper Silurian. *Condylocrinus* Eichwald (1860, p. 612), Devonian. Presumably the ancestral stock of *Spyridiocrinus* is within one of these genera. At any rate, rhodocrinitid ancestry is postulated for *Spyridiocrinus* with little doubt. If these considerations are correct, then the two zygodiplobathrid genera had independent evolutionary histories regardless of the origin of *Cleiocrinus*. Thus zygodiplobathrids were probably polyphyletic. If the ancestry of *Cleiocrinus* can be clarified, it seems advisable to drop the suborder Zygodiplobathrina and group the two genera within the Eudiplobathrina along with the most closely related families.

As previously mentioned, the zygodiplobathrid base is associated with relatively small basals and large infrabasals whereas the reverse characterizes eudiplobathrids. This suggests that one type can be derived from the other by means of 'mutations' which affected the growth of the youngest crinoids; these 'mutations' would increase or decrease the growth rates of the height and width of the basals relative to those of the surrounding plates. [The word 'mutations' is used in a highly general sense, namely to include gene changes, chromosome additions, translocations, etc.; a detailed discussion of this concept is given by Brower (1973, p. 328 et seq.).] In order to test this hypothesis, a series of hypothetical crinoids was drawn based on statistical data (text-fig. 3b–g). A simulated rhodocrinitid larva is pictured in text-fig. 3b; this was reconstructed based on analogy with living crinoids, using the statistical data and plate-growth sequences for camerate crinoids (Brower 1973, pp. 292–328). The subsequent growth of this 'larva' was simulated in two ways. In Case I the growth

rates of the basals are large compared to those of the infrabasals and radials. In Case II the basals are characterized by relatively small rates of growth. Note that the growth rates are only approximate averages for height and width and that the growth rates are listed as proportions. The data are:

Case	Approximate values of subsequent growth rates for height and width of the listed plates relative to total height of the larval calyx			Type of base produced
	Infrabasals	Basals	Radials	
I	0·14	0·43	0·43	Rhodocrinitid–eudiplobathrid (text-fig. 3c)
II	0·62	0·13	0·25	Zygodiplobathrid (text-fig. 3d)

Text-fig. 3b–d indicates that the simulation is geometrically feasible and thus zygodiplobathrids can be derived from eudiplobathrids by a decrease in the growth rates of the basals relative to those of the surrounding plates.

Comparison. Assignment to the Dimerocrinitidae seems probable because the Pentland crinoid is basically a dicyclic camerate crinoid with many fixed-brachials and radials in contact within the lateral interrays. For reasons discussed above, the presence of a zygodiplobathrid base is not thought to be a fundamental character. Considering the affinities of the Pentland species within the Dimerocrinitidae, the most closely allied crinoids should have: (1) four arms per ray with axillary secundibrach 2; (2) primitive structure of the fixed-brachials. In D. pentlandicus primibrach 1 has eight sides and the primaxil eight or nine sides. The most closely related dimerocrinitid should exhibit a similar structure, probably consisting of hexagonal primibrach 1 and septagonal primaxil. (3) Slender calyx. (4) Relatively high infrabasals. Only a few Ordovician and Silurian dimerocrinitids fit these specifications. These include Ptychocrinus parvus (Hall) (Wachsmuth and Springer 1897, p. 199) and several species of Dimerocrinites with four arms in each ray; i.e. specimens from the Wenlock of Gotland and Dudley, England, labelled D. quinquangularis (Angelin), D. ornatus (Angelin), and D. speciosus (Angelin). These crinoids were described by Angelin (1878), but unfortunately the original figures are not reliable because many are probably composites of several crinoids which are not always conspecific; hence, emphasis is placed on specimens seen by the writer. These crinoids are easily separated from D. pentlandicus by the shapes of the primibrachs, the nature of the adjacent interbrachials, and the type of cup base present. The Pentland crinoid has primibrachs with eight or nine sides whereas those of the other taxa bear from four to nine sides. Due to the structure of the primibrachs, D. pentlandicus has four ranges of interbrachials below the proximal secundibrachs but only one, two, or three ranges are found in the other forms. As mentioned above, the Pentland species has a zygodiplobathrid-type base whereas the other crinoids have eudiplobathrid bases, and Ptychocrinus parvus has more prominent median-ray ridges than in D. pentlandicus.

Phylogeny. The most likely ancestor for D. pentlandicus is an Ordovician or lower Llandovery dimerocrinitid or ptychocrinid with four arms in each ray. Two main evolutionary changes were involved. First is the development of a zygodiplobathrid

from a eudiplobathrid base. This probably occurred in roughly the same way that *Spyridiocrinus* was derived from the Rhodocrinitidae, by means of a growth 'mutation' which reduced the growth rates of height and width of the basals relative to those of the sub- and superjacent infrabasals and radials. Variation of this sort is unknown within the Dimerocrinitidae, but precedent for such evolution is shown by variation within various rhodocrinitids such as *Rhipidocrinus crenatus* and the Carboniferous inadunate *Woodocrinus gravis* Wright (1950–1954, pl. 25, cf. figs. 2, 3, 5, 6, 9). Where the basals are small, they are not in lateral contact and the radials rest on the truncated infrabasals. If the basals are large, they are in lateral contact and the radials are fully separated from the infrabasals. Small basals are rectangular like those of *D. pentlandicus* but the large basals are hexagonal like those of normal dimerocrinitids. The simulated crinoids in text-fig. 3*e–g* show that such a change is at least geometrically plausible.

The second change is the divergence in the structure of the primibrachs and interbrachials. Increase in the number of sides of the primibrachs probably began when the plates formed early during ontogeny. The shape changes were achieved through adjustments of the various growth rates of widths of the primibrachs (see Brower 1973, pp. 401–407 for outline of similar evolution in patelliocrinids). An increase in the supply rate of interbrachials in conjunction with the shape changes of the primibrachs mentioned above would be sufficient to develop the interbrachial areas of *D. pentlandicus* from the ancestral type.

<div align="center">

Subclass INADUNATA Wachsmuth and Springer, 1885
Order DISPARIDA Moore and Laudon, 1943
Superfamily HOMOCRINICAE Ubaghs, 1953
Family PISOCRINIDAE Angelin, 1878
PISOCRINUS de Koninck, 1858

</div>

Type species. *P. pilula* de Koninck, 1858.

<div align="center">

Pisocrinus campana Miller

Plate 74, figs. 1, 2, 4; text-fig. 4

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1891   *Pisocrinus campana* Miller, p. 32, pl. 11, figs. 4, 5.
1892   *Pisocrinus campana* Miller, p. 642, pl. 11, figs. 4, 5.
1897   *Pisocrinus* sp., Wachsmuth and Springer, pl. 8, fig. 10.
1915   *Pisocrinus campana* Miller; Bassler, p. 980.
1926*b* *Pisocrinus campana* Miller; Springer, p. 76, pl. 24, figs. 6–27.
1943   *Pisocrinus campana* Miller; Bassler and Moodey, p. 612.
1952   *Pisocrinus* cf. *campana* Miller; Lamont, p. 29.

Scottish material. A crown and a cup (RSM 1970.42.3, 4) occur on a small slab. Unfortunately, the original has been lost and the two crinoids are only represented by latex casts. Two other crowns, RSM 1970.42.2, 1970.43. Part and counterpart of a cup, Hunterian Museum (HM) 3173a, b.

Type locality. Upper Llandovery or Wenlock; Salamonie Dolomite; Wabash, Indiana, U.S.A.

Other American localities. Upper Llandovery; Osgood Formation; St. Paul and adjacent areas in southern Indiana. Lower Wenlock; Laurel Limestone; St. Paul, Indiana. Lower Ludlow; Brownsport Formation; various localities in Wayne, Perry, and Decatur Counties, Tennessee.

Scottish locality. Plectodonta Mudstones, lower part of River North Esk, about 220 yd north-east of the North Esk Reservoir.

Diagnosis. A species of *Pisocrinus* with moderately high cup which shows wide variations in shape, height/width ranges from 0·75 to 1·2; walls of cup slightly rounded; basals high relative to radials regardless of cup shape; radial processes weakly developed; plates of cup smooth. Arms long and slender, arm length/height of cup ranges from 4·0 to 8·0, arms of mature crinoid consist of about five brachials. Dorsal sides of brachials rounded or distinctly triangular. Stem round, composed of only one order of plates; distal columnals nodose.

Description of Scottish specimens. Cup moderately high; height/width ranges from 0·85 to 1·0; sides of cup slightly rounded; basals high relative to cup height; height of basals/cup height equals about 0·41; surfaces of cup smooth, may be faintly rugose in one specimen. Basals five, three pentagonal and two rectangular (*A* ray, *BC* interray); pentagonal basals larger than rectangular ones, height/width of pentagonal basal is 0·8 to 1·0; same for rectangular basal equals 0·5. Large inferradial occurs under *B* and *C* ray radials, septagonal, height/width about 1·0. *B* and *C* ray superradials basically pentagonal, height/width 0·7. *A* and *D* ray radials largest plates in cup, pentagonal to septagonal, height/width ranges from 0·8 to 1·0. *E* ray radial not seen. Radial facets wide, about two-thirds width of radials, faintly curved with small radial processes. Tegmen unknown. Arms large, massive, blade-like, consist of uniserial, non-pinnulate brachials; each arm has from three to eight brachials; most of arm tapers gently; at distal arm tips, the taper angle increases and the last brachial is bullet-shaped; arm length/cup height varies from 4·0 to 5·5. Primibrach *1* small, rectangular, much wider than high, partially set inside of radial processes; higher primibrachs much larger and more massive, sutures obscure; height/width variable, ranges from 1·0 to 16; dorsal sides of brachials are more or less strongly triangular. Large part of column observed, round with small round axial canal; entire column consists of only one order of columnals; column tapers distally from below calyx to mid-distal region of stem; distal-most stem plates become wider than those of mid-distal region. Proximal columnals wide relative to height, shaped like thin discs with slightly nodose edges.

Comparison. Despite the recent monographic treatment of pisocrinids by Bouška (1956), the American species remain in need of revision. For example, *P. campana* Miller (see Springer 1926*b*, p. 76) and *P. benedicti* Miller (1891, p. 29; Springer 1926*b*, p. 77) commonly occur together; the former is separated by a cup with straight or slightly curved walls which is high relative to width whereas the latter is lower and more globose. Springer noted intergradations between the two species (1926*b*, p. 76): 'As stated, with the expanding and bell shaped forms the identification is easy, but those with a lower calyx, ovoid to globose, are confusing; if they have

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EXPLANATION OF PLATE 74

Figs. 1, 2, 4. *Pisocrinus campana* Miller, note blade-like arms, relatively high cup with straight walls and high basals, figured specimens, *Plectodonta* Mudstones, lower part of River North Esk, about 220 yd north-east of the North Esk Reservoir. 1, crown with rugose markings on plates of cup and relatively short arms, *A*, *B*, and *C* ray view of RSM 1970.42.1, ×6·4. 2, poorly preserved crown with tumid plates and cigar-like arms, lateral view of RSM 1970.43, ×7·0. 4, left, relatively wide and globose cup with smooth plates, *A* and *B* ray view of RSM 1970.42.3; right, crown with comparatively high cup with smooth plates and long arms, lateral view of RSM 1970.42.4, ×5·3.

Fig. 3. *Ptychocrinus longibrachialis* sp. nov., note long slender arms composed of elongate brachials, *C* ray view of holotype, Grant Institute of Geology 134, mudstone layer, just above top plantation on Gutterford Burn, ×2·8.

Fig. 5. *Dimerocrinites pentlandicus* sp. nov., note small basals and zygodiplobathrid-type base of cup, shape of primibrachs and structure of interbrachials, lateral view of holotype RSM 1885.26.78h, 'Starfish Bed', Gutterford Burn, ×3·8.
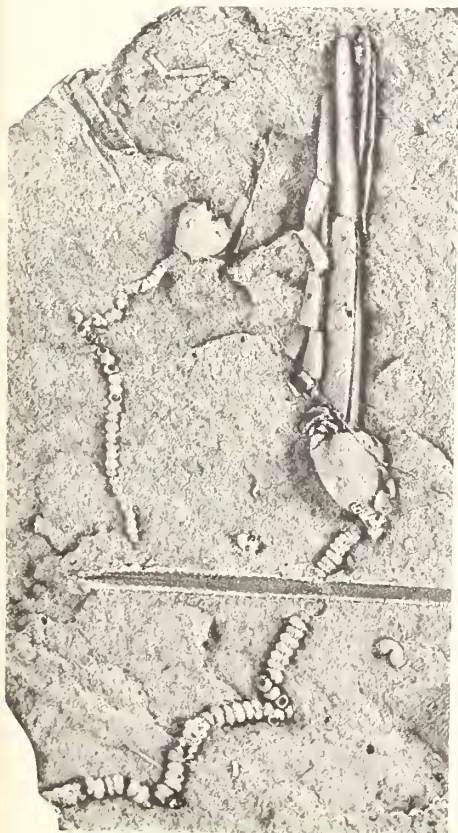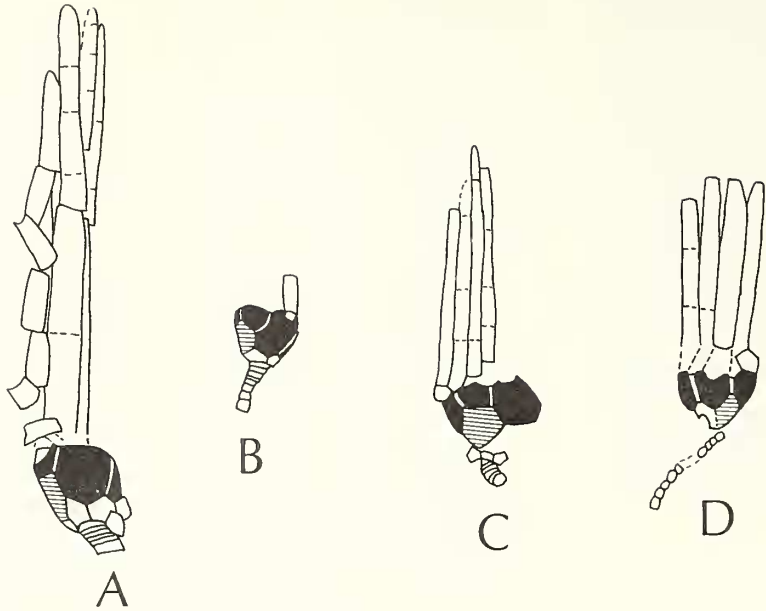
PLATE 74

TEXT-FIG. 4. Figured specimens of *Pisocrinus campana*. Note slender calyx with high basals and long blade-like arms. A, lateral view of crown, RSM 1970.42.4, ×5·3. B, *A* and *B* ray view of cup with a partial arm, RSM 1970.42.3, ×5·3. C, *A*, *B*, and *C* ray view of partially disarticulated crown, RSM 1970.42.1, ×5·0. D, lateral view of RSM 1970.43, ×5·3, the plate structure of the cup is conjectural. Symbols: radials and superradials black, inferradials are ruled horizontally.

fairly high basals, we may call them *campana*, while those with basals but little visible will have to go into *benedicti*. Thus there will be an intermediate zone in which the distinction is shadowy.' This is shown by measurements made on the specimens in the Springer Collection, United States National Museum, in which the height/width ratios of the cup of specimens assigned to *P. campana* by Springer ranges from 0·75 to 1·2 while that of *P. benedicti* varies from 0·60 to 1·2. The figures overlap and further data are required to either recombine or fully define the two species. Pending restudy, the specimens with the higher cups having high basals and straight or nearly straight walls are assigned to *P. campana* while those with lower and more globose cups with shorter basals are placed in *P. benedicti*. Thus *P. campana* is a highly variable species which ranges from the upper Llandovery to the lower part of the Ludlow.

The specimens from the Pentland Hills differ from typical North American individuals in several respects. Most American crinoids have well-developed radial processes although these grade into individuals with faint radial processes (Springer 1926*b*, pl. 24). The Scottish specimens are characterized by shallow radial processes like some of the end-member crinoids from America. The Pentland specimens range much smaller. The largest crown is about 13 mm high whereas Springer (1926*b*, pl. 24, figs. 7, 8) illustrated crowns about 65 mm high. Both the Pentland and the

American crinoids possess comparable numbers of brachials in each arm. The fact that crinoids develop new brachials at the arm tips throughout life indicates the Pentland crowns were probably not juveniles. These are believed to be adults which exhibited reduced growth rates of size with respect to time compared with typical American individuals. Nevertheless, the high cup with slightly rounded walls and large basals in conjunction with the long blade-like arms and nodose columnals in the stem indicate that the Scottish crinoids should be referred to *P. campana.*

P. campana is also closely related to *P. pilula* de Koninck (see Bather 1893, p. 27; Bouška 1956, pp. 13, 62, 104) of the Wenlock and Ludlow of England, Gotland, and Bohemia. Both species are long ranging and widespread and both vary in the height/width ratio of the cup and the nature of the radial processes. *P. campana* can be separated from *P. pilula* by several characteristics. Better-developed radial processes are seen in *P. pilula.* The distal columnals of *P. pilula* exhibit smooth sides whereas the columnals of *P. campana* are nodose. Also the proximal stem of *P. pilula* appears to have been secondarily thickened, a feature which is not known in *P. campana.* The basals of *P. pilula* are always low while those of *P. campana* are much higher relative to the height of the cup. The cup walls of *P. campana* are commonly rounded but those of *P. pilula* are generally straight. *P. pocillum* Angelin (1878, p. 21; Bather 1893, p. 33; Springer 1926b, p. 80) from the Silurian of Gotland, *P. ubaghsi* Bouška 1956 and *P. moŕinensis* Bouška 1956 both from the Ludlow of Bohemia, have higher cups (height/width ranges from 1·3 to 1·7) with straight and angular sides in contrast to the lower cup with straight or slightly rounded walls of *P. campana.*

Superfamily IOCRINICAE Ubaghs, 1953
Family MYELODACTYLIDAE Miller, 1883
HERPETOCRINUS Salter, 1873

Type species. H. fletcheri Salter 1873.

Herpetocrinus parvispinifer sp. nov.

Plate 73, figs. 3, 5

Holotype. RSM 1897.32.285, a terminal coil with part of the straight portion of the stem, in which the crown is only represented by the distal parts of the arms. The lack of the cup and most of the crown does not preclude definite generic and specific placement because all Myelodactylidae can be classified on stems alone: the crowns are only known in three of the five genera assigned to the family by Moore (1962, pp. 40–44).

Paratypes. Straight stem segments with cirri: RSM 1885.26.78e (part and counterpart), 1897.32.286 (part and counterpart). A partial terminal coil and straight stem segment: RSM 1897.32.287 (part and counterpart). A partial terminal coil: RSM 1897.32.288 (part and counterpart).

Derivation of name. From the short spines on the distal margin of each cirral.

Type locality. Gutterford Burn Flagstones, 'Starfish Bed', Gutterford Burn.

Diagnosis. A species of *Herpetocrinus* with characteristic cirral ornamentation; distal end of cirral expanding outward to form small angular rim-like process; typically the rim bears two to six short spines; rarely, the rim is absent or weakly developed but such cirrals always show traces of spines. Column with crescent-shaped cross-section, concave part of crescent faces the outside of the coil of the stem, convex side of crescent located on the inside of the coil.

Description. Proximal part of stem coiled in an S-shaped bend which is followed by another half-circle of coil, distal part of stem nearly straight. Proximal portion of stem round, about 14 mm long, diameter increases from 1·2 to 1·6 mm in distal direction, lacking cirri; longitudinal sutures well developed in middle of stem. Columnals nodose, with parallel sides in straight parts of column; where the column bends, the columnals become slightly wedge-shaped, height/average width of proximal columnals about 0·18. Next part of stem with crescentic cross-section, convex part of crescent occurs on the inside of the coil, concave part of crescent on outside of the coil, diameter of this stem segment increases from 1·8 to 2·8 mm distally, cirri lacking, longitudinal sutures obscure. Columnals slightly nodose, somewhat wedge-shaped, ratio of average height/width ranges from 0·5 to 0·36 with distal columnals having the lowest values. Third region of stem similar to previous part, having crescentic cross-section, diameter of stem segment decreases distally from 3·2 to 2·4 mm, several cirri present in distal part of stem segment, adjacent nodals separated by one or two columnals, longitudinal sutures are poorly developed. Columnals not nodose, proximal columnals slightly wedge-shaped but distal ones have parallel sides, average height/width of columnals ranges from 0·25 to 0·35, internodals lacking cirri; nodals with cirri, portion of nodal with cirrus scar expands, this constricts the adjacent part of the internodal; articular facet for cirrus round, somewhat protuberant. Distal portion of stem almost straight, with crescentic cross-section, width varies from 2·0 to 3·0 mm, cirri generally present, adjacent nodals usually separated by one columnal, longitudinal sutures obscure. Columnals not nodose, like those in previous part of stem except that the sides are parallel and the columnals are not wedge-shaped, average height/width of columnals ranges from 0·35 to 0·30.

Cirri long and slender, longest known cirrus is incomplete, observed length about 30 mm, consisting of forty-one plates. Cirrals with round cross-section, sides expanding distally to form rim-like process which bears two to six short spines, some cirrals lack rims but some spines are always present. Crown only known from distal brachials; brachials uniserial, lacking pinnules, ranging from equidimensional to higher than wide. Distal part of column not observed.

Comparison. The Pentland species is most closely related to *H. fletcheri* Salter (1873, p. 118; Bather 1893, p. 46; Springer 1926*b*, p. 86; 1926*a*, p. 10; Moore 1962, p. 42) from the Wenlock of Great Britain and Gotland. In *H. fletcheri* the cirrals are evenly nodose whereas those of *H. parvispinifer* generally possess small angular distal rims which commonly bear two to six short spines or spine bases. The Pentland individuals exhibit some variability in the nature of the cirrals while the distal rims range from prominent to weakly developed or absent, but these are normally seen. The number of spines varies in increments of two, either two, four, or six. When four or six are present, the two spines lying within the plane of stem coil are generally the best developed. *H. parvispinifer* is distinguished from the Gotland *H. flabellicirrus* Bather, 1893 by the shape of the individual cirrals, these being nodose in the Gotland form and rim and spine bearing in the Pentland animal. Also, the cirri of *H. flabellicirrus* are ponderous and expand distally whereas those of *H. parvispinifer* are more slender and taper evenly distally. The Pentland species differs from *Myelodactylus* in the cirri, which in myleodactylids are elongate and unornamented, but the cirrals of the Pentland herpetocrinid are wider and either nodose or rim and spine bearing. Also, the longitudinal sutures are well developed throughout the stem of *H. parvispinifer* whereas they tend to disappear on the distal end of the column of *Myleodactylus*.

<div align="center">

Order CLADIDA Moore and Laudon, 1943
Suborder DENDROCRININA Bather, 1899
Family DENDROCRINIDAE Miller, 1899
DENDROCRINUS Hall, 1852

</div>

Type species. D. longidactylus Hall, 1852.

Dendrocrinus extensidiscus sp. nov.

Plate 75, figs. 1–3; text-fig. 5

Holotype. A well-preserved crown of a young specimen with an attached stem segment on RSM 1897.32.289.

Paratypes. Young crowns: RSM 1897.32.290, 291. Long stem segment with partial cup of a young crinoid on RSM 1897.32.289. Cup of mature specimen with a long stem segment: RSM 1885.26.78g. Stem segment with attached cirrus roots: RSM 1897.32.301.

Derivation of name. In allusion to the relatively high columnals.

Type locality. Gutterford Burn Flagstones, 'Starfish Bed', Gutterford Burn.

Diagnosis. A species of *Dendrocrinus* with relatively slender cup, brachials high with respect to width; column round; distal columnals have relatively large ratios of height/width compared to most dendrocrinids.

Description. Cup conical with straight walls, height/width ranges from 0·8 to 1·0. Plates of cup convex with depressed sutures, otherwise smooth. Infrabasals high, pentagonal, higher than wide, infrabasal circlet occupies from 17 to 24% of the cup height. Basals large, lateral interray basals hexagonal, higher than wide, height of basal circlet ranges about 50% of the cup height. *CD* interray basal septagonal, largest plate in cup, distally truncated for reception of anal X. Radials basically pentagonal, equidimensional or wider than high, radial circlet generally represents about 30% of the cup height. Radial facets smooth, narrow, horseshoe-shaped, sloping outward, width of facet varies from 45 to 60% of the width of the radial. Radianal poorly known, large, lying under *C* ray radial. *C* ray radial pentagonal with wide radial facet, located above radianal and between anal X and *B* ray radial. Anal X five-sided, occurring between *C* ray radial, radianal, and *D* ray radial and above truncated *CD* interray basal. Arms only known in young crinoid, slender, branching isotomously, once or twice; usually six primibrachs present, rarely five or seven plates occur, distal primibrach is axillary; number of secundibrachs uncertain, twelve plates present in unbranched arm segment, branched arm segment probably has roughly the same number of secundibrachs; from one to three tertibrachs present. Brachials uniserial, nonpinnulate, smooth, slender, with round or sharp backs. Nonaxillary primibrachs rectangular; primibrach *1* is shortest primibrach, height/width ranges from 0·7 to 1·2; other nonaxillary primibrachs much higher, height/width varies from 1·7 to 4·0; axillary primibrach pentagonal, spear-shaped, height/width ranges from 1·6 to 2·3. Secundibrachs higher than wide, height/width equals from 2·0 to 3·3. Column round, composed of smooth columnals that are high relative to width compared to other species of *Dendrocrinus*, column lacking cirri, only one order of columnals can be differentiated. Proximal columnals which are immediately below the calyx disc-shaped, much wider than high, height/width varies from 0·2 to 0·5. Distal columnals of young specimens much higher than wide, height/width ranges from 1·7 to 4·0. Distal columnals of adult have height/width ranging from 0·25 to 0·8. Columnals near rooting device have strongly crenulate sutures, height/width of columnals is about 0·5. Rooting device partially known, consisting of at least two heavy cirri, each of which branches several times.

Remarks. This species is represented by cups which fall into two height intervals. The largest crinoid has a cup height of 8·0 mm. The smaller crowns range from 1·1 to 2·0 mm in cup height. The large specimen is considered conspecific with the smaller ones because of similarities in outlines of the cup and its component plates and because all specimens have similar convex plates with depressed sutures. The main differences between the young and mature specimens are in the column. Distal columnals of the smaller specimens are much higher than wide and the height/width ratios of these plates range from 1·7 to 4·0. The equivalent ratios for the adult crinoid vary from 0·25 to 0·8 indicating columnals that are wider with respect to height. The columnals of the mature crinoid are higher than in the young specimens. The difference in shape of the columnals between the young and adult specimen is attributed

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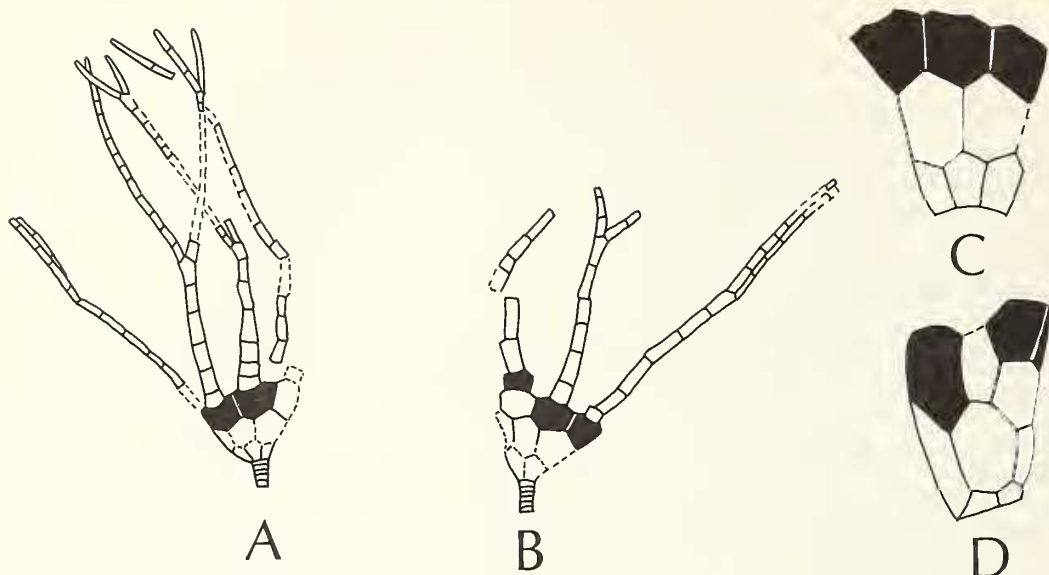
TEXT-FIG. 5. *Dendrocrinus extensidiscus* sp. nov. A, B, *D* and *B* ray views of holotype, counterpart and part, respectively; note relatively long and slender arms with elongate brachials; the cup is crushed so that the plates appear wider than in uncrushed specimens; if the crinoid is interpreted correctly, the *C* ray radial is located above the radianal and well above the other radials, this is higher than in normal specimens and the holotype is considered abnormal in this respect, ×4·9. C, D, lateral ray view of external mould and *CD* interray view of internal mould, paratype RSM 1885.26.78g, ×3. The radials are black.

to progressive growth. In most crinoids the height/width ratios of columnals decrease as the columnals become older and larger (Brower 1973, pp. 298, 299). The arms are not known in the larger crinoid and these cannot be compared with those of younger specimens.

Comparison. D. extensidiscus is only remotely related to the Wenlock age species from North America. These include: (1) *D. longidactylus* Hall (1852, p. 193) which has a cup with slightly rounded walls and more numerous arm branches; (2) *D. celsus* Ringueberg (1888, p. 132) which shows eleven primibrachs (compared to about six in this form), more arm branches, and a column which expands near the calyx; and

EXPLANATION OF PLATE 75

Figs. 1–3. *Dendrocrinus extensidiscus* sp. nov., note relatively high columnals and slender arms consisting of elongate brachials, 'Starfish Bed', Gutterford Burn. 1, *D* ray view of holotype RSM 1897.32.289 (counterpart, a well-preserved young crown with long stem segment) and paratype RSM 1897.32.289 (crushed cup of young specimen with long stem segment showing well-preserved columnals, located on right side of photograph), ×4·2. 2, *C* ray view of holotype RSM 1897.32.289 (part), ×4·2. 3, lateral view of a mature specimen, paratype RSM 1885.26.78g, ×1·4.

Figs. 4, 5. *Macrostylocrinus silurocirrifer* sp. nov. 4, stem segment with well-preserved cirri, paratype RSM 1897.32.293, 'Starfish Bed', Gutterford Burn, ×2·4. 5, lateral view of immature crinoid, paratype GSE 12791, Deerhope Burn Flagstones, River North Esk, at bend 935 yd N. 30° W. of North Esk Cottage, ×4·8.
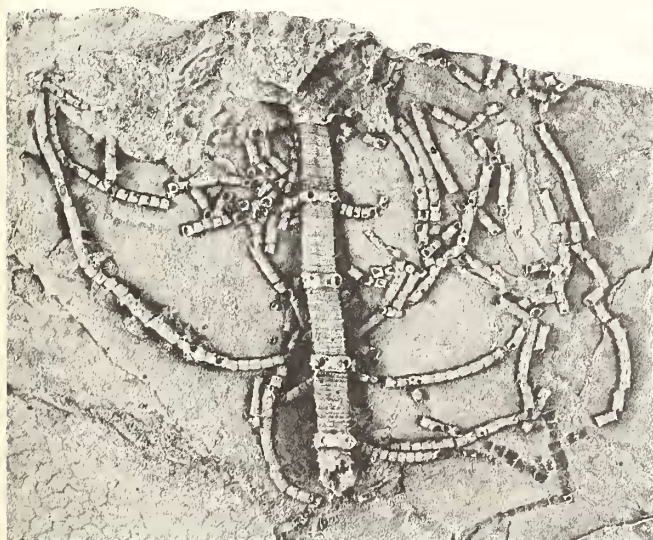
PLATE 75

(3) the peculiar *D.? nodobrachiatus* Ringueberg (1890, p. 303) which is probably not referable to *Dendrocrinus* because either ramules or pinnules are present according to Ringueberg: also the cup is wider and there are only two main arms per ray with primibrach 3 forming the axillary. In addition, *D. extensidiscus* differs from all other Silurian species by the relatively long and slender columnals and brachials.

Only two other species of *Dendrocrinus*, *D. rugocyathus* Ramsbottom (1961, p. 16) and *D. granditubus* Ramsbottom (1961, p. 15), are known from Britain; both are upper Ordovician. They are characterized by stellate plates in the cup and a pentalobate stem. In *D. extensidiscus* smooth calyx plates and a round stem are observed. The two British Ordovician species are closely related to the American upper Ordovician *D. casei* Meek (1871, p. 295; 1873, p. 28). This American form has very similar calyx ornament and shape, stem type, and general stem and crown habit to the British Ordovician crinoids.

The most similar crinoids consist of a series of middle and upper Ordovician forms from North America. In general, these and the Pentland animal resemble each other in having round stems which are non-nodose, similar calyx shapes with smooth plates and slender arms which branch two to four times. Middle Ordovician forms in this category are: (1) *D. acutidactylus* Billings (1857, p. 266; 1859, p. 37); (2) *D. gregarius* Billings (1857, p. 265; 1859, p. 36); and (3) *D. gracilis* (Hall) (1847, p. 84). Upper Ordovician species are: (1) *D. navigiolum* Miller (1880, p. 235) and (2) *D.? sp. nov. aff. D.? navigiolum* Brower (1973, p. 457). Of all the above species, *D. acutidactylus* is judged the closest with respect to over-all morphology. *D. extensidiscus* is separated from all the above species by the higher, relative to width, columnals and brachials. Therefore the affinities of the Pentland crinoid lie closer to Ordovician forms than to Silurian ones.

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